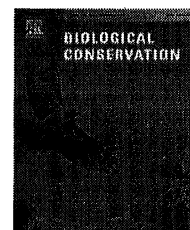




available at www.sciencedirect.com



journal homepage: www.elsevier.com/locate/biocon



Effects of habitat loss and fragmentation on amphibians: A review and prospectus

Samuel A. Cushman*

USDA Forest Service, Rocky Mountain Research Station, P.O. Box 8089, Missoula, MT 59801, USA

ARTICLE INFO

Article history:

Received 17 March 2005

Received in revised form

26 September 2005

Accepted 29 September 2005

Available online 7 November 2005

Keywords:

Habitat loss

Habitat fragmentation

Amphibians

Dispersal

Persistence

Extinction

Review

ABSTRACT

Habitat loss and fragmentation are among the largest threats to amphibian populations. However, most studies have not provided clear insights into their population-level implications. There is a critical need to investigate the mechanisms that underlie patterns of distribution and abundance. In order to understand the population- and species-level implications of habitat loss and fragmentation, it is necessary to move from site-specific inferences to assessments of how the influences of multiple factors interact across extensive landscapes to influence population size and population connectivity. The goal of this paper is to summarize the state of knowledge, identify information gaps and suggest research approaches to provide reliable knowledge and effective conservation of amphibians in landscapes experiencing habitat loss and fragmentation. Reliable inferences require attention to species-specific ecological characteristics and their interactions with environmental conditions at a range of spatial scales. Habitat connectivity appears to play a key role in regional viability of amphibian populations. In amphibians, population connectivity is predominantly effected through juvenile dispersal. The preponderance of evidence suggests that the short-term impact of habitat loss and fragmentation increases with dispersal ability. However, species with limited dispersal abilities are likely to be equally imperiled by habitat loss and fragmentation over longer time periods. Rigorous understanding of the effects of habitat loss and fragmentation on amphibians will require species-specific, multi-scale, mechanistic investigations, and will be benefit from integrating large empirical field studies with molecular genetics and simulation modeling. Molecular genetic methods are particularly suited to quantifying the influences of habitat structure across large spatial extents on gene flow and population connectivity. Conservation strategies would benefit by moving from generalizations to species and process specific recommendations and by moving from site-specific actions to implementing conservation plans at multiple scales across broad landscapes.

© 2005 Elsevier Ltd. All rights reserved.

1. Introduction

1.1. The extinction crisis and amphibians

Earth is facing the largest mass extinction in 65 million years (Lawton and May, 1995; Vitousek et al., 1997; Wilson, 1999;

Myers and Knoll, 2001; Balmford et al., 2003). Current global extinction rates for animals and plants are estimated to be up to 1000 times higher than the background rate in the fossil record (Wilson, 1999; Baillie et al., 2004). Vertebrate animal taxa are disappearing at disproportionately high rates, and amphibians are the group with the highest proportion of

* Tel.: +1 406 546 6379.

E-mail address: scushman@fs.fed.us.

0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2005.09.031

species threatened with extinction (Stuart et al., 2004; Beebee and Griffiths, 2005). The 2004 IUCN red list of threatened and endangered species identifies one in three of the world's amphibian species as threatened with extinction (Baillie et al., 2004).

1.2. Vulnerability of amphibians

The apparent vulnerability of amphibians (Pechmann et al., 1991; Houlahan et al., 2000; Kiesecker et al., 2001; Baillie et al., 2004) may be due to a complex of factors, including: (1) relatively low vagilities, which amplifies the effects of habitat fragmentation (Sinsch, 1990; Gibbs, 1998; deMaynadier and Hunter, 2000; Bowne and Bowers, 2004), (2) high vulnerability to death when moving across roads and through inhospitable terrain, which depresses population growth rates (Fahrig et al., 1995; Carr and Fahrig, 2001; Carr et al., 2002), (3) often narrow habitat tolerances, which exacerbates the effects of habitat loss, degradation, and edge effects (Findlay and Houlahan, 1997; Semlitsch, 2000; Houlahan and Findlay, 2003), and (4) high vulnerability to pathogens, invasive species, climate change, increased ultraviolet-B exposure and environmental pollution (Pounds et al., 1999; Broomhall et al., 2000; Kiesecker et al., 2001; Blaustein et al., 2000; Hecnar, 1995; Bridges and Semlitsch, 2000; Davidson et al., 2001; Stuart et al., 2004).

1.3. Importance of habitat loss and fragmentation

Habitat loss and fragmentation contribute directly to most of these threats (Carr and Fahrig, 2001; Bowne and Bowers, 2004; Houlahan and Findlay, 2003). Recent research has provided information on the relationships between certain amphibians and certain attributes of habitat loss and fragmentation, and has clearly implicated the effects of habitat fragmentation on juvenile dispersal as one of the key issues in the conservation of pond breeding amphibians (Sjögren, 1991; Sinsch, 1992; Sjögren-Gulve, 1994; Vos and Chardon, 1998). However, most studies of the influences of habitat loss, fragmentation, or related mortality risks have not provided clear insights into the population-level implications of these impacts (Carr et al., 2002). There is a clear need for studies that focus on the mechanisms that drive patterns of distribution and abundance (Marsh and Trenham, 2001; Bowne and Bowers, 2004).

1.4. Moving from sites to landscapes; ponds to populations

In order to understand the population-level implications of habitat loss and fragmentation, it is necessary to move from site-specific inferences to assessments of how multiple factors interact across large spatial extents to influence population size and population connectivity (Ruggiero et al., 1994; McGarigal and Cushman, 2002; Bowne and Bowers, 2004). Non-spatial studies conducted at local scales do not provide a basis for inferences at the landscape or regional level (McGarigal and Cushman, 2002). There is often a gross mismatch between the scale of ecological research and population-level responses (Kareiva and Anderson, 1988; Ruggiero et al., 1994). For example, correlations between organism

abundance and the area of various landcover types within a certain distance of a breeding pond does not provide information necessary to infer how habitat patterns interact with the spatial distribution of breeding ponds to influence distribution and abundance. Landscape-level studies that represent the spatial patterns of the environment in a manner relevant to the organisms of question, and that address species-specific movement and abundance characteristics are essential to extend fine-scale species environment relationships to the population-level (McGarigal and Cushman, 2002).

1.5. Purpose and goals

The overall goal of this paper is to summarize the state of knowledge, identify information gaps and suggest approaches to provide reliable knowledge and effective conservation of amphibians in landscapes experiencing habitat loss and fragmentation. The paper is divided into four major components. The first is a review of current knowledge about relationships between habitat loss and fragmentation and pond-breeding amphibian populations at landscape and regional scales. Using this review as context, the second section identifies some important information gaps and research needs. Next, I propose several research approaches that may be effective at filling these information gaps. Then, I suggest several ideas to link research more effectively to conservation, and suggest interim conservation strategies.

2. The state of knowledge

2.1. Habitat area in uplands

Relatively few landscape-level studies of amphibian density and movement have been conducted (Houlahan et al., 2000; McGarigal and Cushman, 2002). Most existing studies have focused on relationships between forest cover and species occurrence. These have shown positive relationships between amphibian populations and area of forest in the surrounding landscape (Dupuis and Steventon, 1999; Knutson et al., 1999; Guerry and Hunter, 2002; Houlahan et al., 2000; Trenham and Shaffer, 2005), and negative relationships with urban development (Delis et al., 1996) and roads (Fahrig et al., 1995; Carr et al., 2002). Studies of landscape composition effects have found relationships between forest cover and amphibian presence at spatial scales ranging from 100 m to over 3000 m radii (Hecnar and M'Closkey, 1997; Knutson et al., 1999; Lehtinen et al., 1999; Guerry and Hunter, 2002; Houlahan et al., 2000; Trenham and Shaffer, 2005). Several studies also note a general pattern of increased species richness with increasing forest cover (Gibbs, 1998; Kolozsvary and Swihart, 1999; Houlahan et al., 2000).

Despite these generalizations, reliable inferences about habitat area effects require attention to species-specific ecological characteristics and their interactions with environmental conditions at a range of spatial scales. Species-specific characterization of habitat is essential if scientists are to evaluate the effects of habitat loss on populations. For example, the suggestion that forest cover in the landscape benefits amphibians may not apply to species that are fully aquatic or that depend on nonforested upland habitat. Also, some

populations of amphibians have been enhanced by human construction of ponds and wetlands in areas where breeding sites were previously limited, such as arid environments. In addition, the location and slope of critical thresholds in habitat amount are species specific, and related to reproductive potential, dispersal ability, home range size, habitat specificity, and other characteristics (Monkkonen and Reunanen, 1999; Fahrig, 2001). Thus, it is essential to explicitly link the habitat tolerances of a species to the extent and pattern of those habitats in the landscape if one is to produce reliable inferences about relationships between habitat area and species distributions.

2.2. Habitat isolation

Several studies have suggested that habitat area is often more important than habitat configuration (Fahrig, 1998, 2003; Cushman and McGarigal, 2004). The evidence for amphibians is equivocal on this question. Guerry and Hunter (2002) found positive associations between nine amphibian species, area of forested habitat and proximity of ponds to forest habitat. Seven of the nine species were associated with forest area. Three of the nine were associated with pond-forest adjacency. This indicates that habitat area and isolation are both important, and that the degree of importance is a species-specific property which likely reflects a combination of life-history and behavioral characteristics.

A growing body of work suggests that roads can have substantial negative effects on amphibian persistence (Vos and Chardon, 1998; Carr and Fahrig, 2001). Habitat fragmentation by roads and other barriers decreases dispersal (Gibbs, 1998; deMaynadier and Hunter, 2000), increases mortality (Fahrig et al., 1995; Carr and Fahrig, 2001) and reduces genetic diversity (Reh and Seitz, 1990). Habitat fragmentation leads to reduced patch size patches, increased patch isolation, and increased risk of demographic, stochastic and genetic events. This increases extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Lande, 1988; Sjögren-Gulve, 1994).

2.3. Connectivity: a key to persistence

A number of researchers have proposed that habitat connectivity is a key to regional viability of amphibian populations (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Semlitsch and Bodie, 1998; Skelly et al., 1999; Marsh and Trenham, 2001; Rothermel and Semlitsch, 2002). Amphibians generally have lower rates of movement per generation than invertebrates, mammals or reptiles (Bowne and Bowers, 2004). Low recruitment of dispersing individuals probably plays a major role in decline and extinction of amphibian populations in fragmented landscapes (Sjögren, 1991; Sinsch, 1992; Sjögren-Gulve, 1998; Vos and Chardon, 1998; Bulger et al., 2003). Breeding sites lacking connectivity to suitable terrestrial habitat may be population sinks due to high mortality of juveniles during emigration (Rothermel, 2004). A number of studies have indicated that populations may decline if immigration is prevented (Brown and Kodric-Brown, 1977; Harrison, 1991) and may not be recolonized following a local extinction (Sem-

litsch and Bodie, 1998). Connectivity seems to be of particular importance as even in unfragmented landscapes, amphibian populations experience relatively frequent local extinction and turnover (Edenham, 1996; Hecnar and M'Closkey, 1996; Alford and Richards, 1999; Trenham et al., 2003). Thus, dispersal is critical for recolonization of local populations and maintenance of regional populations (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Skelly et al., 1999).

2.4. Role of juvenile dispersal in population connectivity

In amphibians, population connectivity is predominantly effected through juvenile dispersal (Madison, 1997; Preisser et al., 2001; Guerry and Hunter, 2002; Rothermel, 2004). Many studies have indicated that post-metamorphic dispersal contributes more to regional persistence than does adult dispersal (Sinsch, 1992, 1997; Sinsch and Seidel, 1995). For example, Preisser et al. (2001) found that adults of a variety of amphibian species move up to 125 m from breeding ponds, while juvenile *Ambystoma* sp. salamanders dispersed up to 670 m, and Wood frog (*Rana sylvatica*) over 1000 m. From this they concluded that juvenile dispersal is essential for landscape connectivity for these species. Other studies have reached similar conclusions based on the relatively small movement distances and philopatry of adults and relatively large dispersal distances of juveniles (Breden, 1987; Berven and Grudzien, 1990).

2.5. Effects of fragmentation on population connectivity

There are several important implications of habitat fragmentation on species persistence. First, a number of studies have shown that high levels of post-metamorphic survival are often required to maintain local populations. For example, one study found that survival to first reproduction had to exceed 18% in order to maintain local populations of the California tiger salamander (*Ambystoma californiense*) (Trenham et al., 2000). However, as they report survival to maturity of less than 5%, they conclude their study population is a sink that would be doomed to extinction in the absence of substantial immigration. In addition, a population model developed for marbled salamander (*Ambystoma opacum*) suggested that post-metamorphic survival had to exceed 70% to maintain local populations (Taylor and Scott, 1997). Second, a number of studies have shown substantial reductions in dispersal success and juvenile survival in fragmented landscapes. For example, Rothermel (2004) found an average of only 9% of juvenile spotted salamander (*Ambystoma maculatum*) released 50 m from a forest edge survived their initial migration to forest. Habitat loss and fragmentation can substantially reduce the abilities of juvenile amphibians to disperse across landscapes and the resulting reductions in post-metamorphic survival and population connectivity can threaten viability.

Recently, a number of studies have investigated the relationships between landscape structure and amphibian dispersal with experimental methods. Both spotted salamanders and wood frogs avoid crossing fields, pastures, clearcuts, lawns, and roads (Windmiller, 1996; Gibbs, 1998; deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Regosin et al., 2003; Marsh et al., 2004). Wood frogs have also been

shown to orient toward forest (deMaynadier and Hunter, 1999). Rothermel and Semlitsch (2002) studied the orientation and movement of several amphibian species in open field and forest environments. They found that orientation of spotted salamander and wood frog is biased toward forest. Spotted salamanders moved three times as far into forest as into fields (Rothermel and Semlitsch, 2002). Lower recapture rates in fields reflected high mortality rates due to desiccation and predation. Also, avoidance of open-canopy habitats by juvenile American toads (*Bufo americanus*) indicates that predictions of dispersal behavior based on adult habitat use may be misleading (Rothermel and Semlitsch, 2002). Rothermel (2004) conducted an experimental study of movement of spotted salamanders and American toads in grass fields at distances of 5 or 50 m from a forest edge. Less than 15% of salamanders and toads released 50 m from the forest edge reached forest, suggesting that few juvenile amphibians would be able to migrate greater distances across pastures (Rothermel, 2004). The authors conclude that fields are substantially resistant, and thus forest fragmentation reduces dispersal rates for these species (Rothermel and Semlitsch, 2002; Marsh et al., 2004; Rothermel, 2004).

Recent research has also suggested that the short-term impacts of habitat fragmentation often increase both with population size and dispersal ability, but particularly strongly with increasing dispersal ability (Gibbs, 1998; Newcomb Homan et al., 2004). This pattern is opposite to what many researchers expect on theoretical grounds, namely that species with larger populations and larger dispersal abilities will be less impacted by fragmentation due to their relatively greater abilities to disperse between breeding sites in fragmented landscapes. For example, in a study of five amphibian species across a gradient of habitat loss, Gibbs (1998) found that organisms with low dispersal rates had better persistence in landscapes with low habitat area. This effect has also been seen in comparison of wood frog and spotted salamander habitat occupancy (Newcomb Homan et al., 2004). A possible explanation is that greater dispersal ability results in greater mortality risk in fragmented landscapes. Carr and Fahrig (2001) suggest that highly vagile organisms may be at a disadvantage in landscapes with roads because of increased likelihood of mortality. An example of this may be the response of red-spotted newt (*Notophthalmus viridescens*) in fragmented landscapes (Guerry and Hunter, 2002). Red-spotted newts appear to have high sensitivity to habitat loss and forest fragmentation. In one study, they were the first species to disappear from a fragmented landscape (Gibbs, 1998). The terrestrial stage of red-spotted newts may last seven years (Forrester and Lykens, 1991) in which they may travel long distances from the natal pond (Gill, 1978). Declines in fragmented landscapes are probably often related to elevated losses of juveniles in the terrestrial period (Gibbs, 1998). The preponderance of evidence suggests that the short-term impact of habitat loss and fragmentation increases with dispersal ability. In a fragmented landscape individuals of species with large dispersal abilities will generally encounter roads and other anthropogenic barriers at higher rates than less vagile species. This will tend to increase mortality rates for these species. The combined effects of roads and land-cover may result in high rates of death among dispersing

juveniles, which can imperil local and regional populations by decreasing recruitment (Sinsch, 1992, 1997; Sinsch and Seidel, 1995).

It appears that species with large dispersal abilities and those with relatively small dispersal abilities are both threatened by habitat loss and fragmentation, but in different ways. Those with large dispersal abilities are vulnerable to elevated dispersing mortality, which appears sufficient to lead to local extinctions (Hecnar and M'Closkey, 1996; Semlitsch et al., 1996; Skelly et al., 1999). However, species with limited dispersal abilities are likely to be equally imperiled by habitat loss and fragmentation over longer time periods. Once these local populations are isolated by fragmentation they may be ultimately doomed to extinction. Amphibian populations experience relatively frequent extinction and turnover (Edenham, 1996; Hecnar and M'Closkey, 1996; Alford and Richards, 1999; Trenham et al., 2003), thus population connectivity is ultimately important even for populations of species that are not directly impacted by habitat loss or elevated mortality risks in dispersing.

3. Challenges to general knowledge

3.1. Lack of species-level information

Despite these generalizations, there are several obstacles that must be overcome before scientists will be able to reliably predict population-level responses of specific species to changes in habitat area or isolation. In most parts of world, there is very limited knowledge of the species–environment relationships of amphibians, their responses to habitat loss and fragmentation and the factors controlling population connectivity (Hazell, 2003). Knowledge is still quite rudimentary about the population-level implications of habitat area, edge, isolation, and road mortality relationships. The precision of knowledge about the habitat relationships, life-history, vagility and behavior of most amphibian species is insufficient. Few studies report population level effects of inter-patch movement and few document movement rates (Bowne and Bowers, 2004). In addition, those studies that do measure movements rarely produce results that can be generally applied, as dispersal data are highly sensitive to sampling scheme and landscape characterization (Carr and Fahrig, 2001). Amphibians exhibit a great range of habitat requirements and dispersal abilities (Stebbins and Cohen, 1995). Little is known about the factors influencing dispersal (Rothermel and Semlitsch, 2002; Rothermel, 2004). Information about the dispersal abilities and relative cost or risk of crossing various landcover types is insufficient for most species to reliably model responses to real landscape mosaics. Additional research is needed to determine appropriate threshold distances and cover-class resistance values for migrating amphibians (Rothermel, 2004). Furthermore, the high variability of population sizes through time confounds efforts to isolate mechanisms through correlative means (Alford and Richards, 1999). The combination of variable population sizes and imprecise knowledge of dispersal parameters and habitat tolerances presents a daunting challenge for researchers attempting to infer population-level impacts of habitat loss and fragmentation on amphibians.

Another obstacle to population-level predictions is that few landscape level studies of habitat fragmentation effects have been conducted. McGarigal and Cushman (2002) reviewed 134 papers on habitat fragmentation published between 1995 and 2000. They identified a paucity of experimental studies at the landscape-level. Most studies were patch-based, and poorly replicated or unreplicated, which greatly limits the inferences that can be reliably drawn. Importantly, they identified amphibians and reptiles as the animal taxa most poorly studied, accounting for only 4% of papers on the effects of habitat fragmentation.

4. Research needs

4.1. Importance of species-specific, multi-scale, mechanistic investigations

Survival of amphibian populations in fragmented landscapes depends on the interaction between the pattern of roads, landcover types, the distribution of breeding ponds, the population sizes in those ponds and the dispersal characteristics of the species (Fahrig, 1998; Carr and Fahrig, 2001). For example, Porej et al. (2004) emphasize the importance of considering scaling differences among species and the structure of the landscape mosaic when investigating thresholds and minimum patch sizes. Furthermore Marsh and Trenham (2001) suggest that pond isolation is often better explained by details of the structure of terrestrial habitats than the distribution of breeding habitats in that landscape, and urge researchers to focus on mechanisms underlying patterns of dispersal and abundance. Petranka et al. (2004) found that there is often a lack of demographic independence within clusters of local breeding ponds, and that the degree of spatial synchrony in local populations varied between species and in response to localized disturbances. Predicting such effects would require information about species specific responses to disturbance, population sizes, movement rates and abilities. Both Monkkonen and Reunanen (1999) and Fahrig (2001) predicted that the location and slope of critical thresholds in habitat amount should be species-specific, and based on a variety of traits including reproductive potential, emigration success, home range size, habitat specificity, dispersal ability and other behaviors.

Each species experiences and responds to ecological conditions in its environment uniquely. Thus, reliable understanding of interactions between species and their environments requires careful attention to both scale and the characterization of the environment. First, species-environment relationships may differ greatly among species across scales (Cushman and McGarigal, 2004). The environmental patterns that are important at one scale for a species may not be those that influence it at coarser or finer scales (Grand and Cushman, 2003). Thus, researchers must adopt multi-scale approaches that allow for assessment of the interaction of environmental patterns across scales (Wiens, 1989; Cushman and McGarigal, 2003). Second, the environment is experienced differently among species. Thus, researchers should select and characterize the environmental attributes on a species-specific basis. For amphibians, this often means assessing interrelationships between multiple environmental

attributes, across a range of scales, for entire landscapes containing dozens or hundreds of local breeding populations. Only by analyzing species-relevant habitat patterns at scales relevant to the populations of those species will it be possible to obtain reliable inferences about the impacts of habitat loss and fragmentation on amphibian populations (McGarigal and Cushman, 2002).

5. Research approaches

5.1. Empirical approaches

There are at least four major ways that one could empirically test relationships between the presence or movement of a particular species and environmental structure at the landscape-level. First, one could conduct large-scale, correlative studies of distribution in relation to habitat composition and configuration at a range of scales (Hecnar and M'Closkey, 1996; Knutson et al., 1999; Kolozsvary and Swihart, 1999; Valan, 2000; Guerry and Hunter, 2002; Weyrauch and Grubb, 2004). Such studies, if replicated sufficiently at the landscape level, can provide reliable information about relationships between landscape structure and the distribution of specific amphibians. The major challenges to such studies are obtaining sufficient replication at the landscape-level to achieve reasonable statistical power, sampling sufficiently large landscapes to allow adequate consideration of environmental patterns at a range of spatial scales, and representing environmental conditions and landscape structures in manners that are relevant to each species in question (McGarigal and Cushman, 2002). These types of studies are also limited in inference because they do not directly measure biological responses such as mortality, movement and productivity. Presence does not always equate to quality. Patterns of distribution do not necessarily reflect patterns of fitness with respect to environmental gradients and landscape patterns.

Two alternative approaches are mark-recapture and telemetry studies (deMaynadier and Hunter, 1999; Rothermel and Semlitsch, 2002; Rothermel, 2004). By quantifying movement rates, distances and routes of dispersing juveniles through complex environments researchers can describe species-specific responses to environmental conditions. Importantly, these methods are well suited for incorporation in manipulative field experiments in which the area and configuration of habitat are controlled to isolate the effects of habitat loss and fragmentation on organism movement and survival rates. These kinds of studies provide the most reliable inferences about relationships between survival rates, movement and ecological conditions (McGarigal and Cushman, 2002). The challenge in these studies is one of cost and sample sizes. Large-scale manipulative field experiments and mark-recapture metapopulation studies are exceptionally expensive to implement, take a number of years to produce reliable results, and generally do not provide large landscape-level sample sizes due to financial and logistical constraints. Likewise, telemetry studies are often limited by spatial scope, sample size and pseudoreplication (Litvaitis et al., 1994).

A fourth alternative involves using molecular genetic methods to empirically derive rates of gene flow among ponds and effective population sizes (Schwartz et al., 1998;

Manel et al., 2003; Curtis and Taylor, 2004; Funk et al., 2005). Molecular genetic methods offer a particularly attractive approach to quantifying gene flow across heterogeneous landscapes, as the logistical and financial costs of extensive mark-recapture study grids are obviated. The genetic characteristics of subpopulations at each sampled pond can provide both information on its effective population size and the degree to which it differs genetically from other ponds. Such methods allow one to quantify rates of gene flow between ponds, assuming time lags between landscape change and genetic response have been accounted for. This in turn allows researchers to test specific hypotheses about the role of specific landscape features and environmental conditions in affecting population connectivity (Manel et al., 2003).

5.2. Simulation models

Simulation models offer a flexible way to investigate the behavior of idealized ecological processes in idealized landscapes. It is important to understand that this idealization in simulation modeling is both a limitation and an asset. It is a limitation in that a simulation is never equivalent to the phenomena being simulated. Decisions are made on which processes to include, at which scales, their relative weights, the functional structure of each and how they interact. Similarly, decisions are made on how to represent the structure and composition of landscapes and how to represent the behavior and ecology of organisms. These decisions fundamentally determine the results, and error in them results inevitably in error in the predictions.

However, the fact that such decisions determine results can also be an advantage. By varying functional parameters, environmental characterization, and organism attributes, scientists can investigate hypotheses about the relative influence of different factors, their interactions, and ranges of organism characteristics, such as gradients of population size or dispersal ability. This provides a means for thorough evaluation of complexes of factors that would be impossible to investigate directly in the field.

5.3. Integrating simulation models and empirical field studies

Simulation results are not compelling unless verified by empirical data. Reliable model predictions depend on accurate algorithmic implementation of the process–pattern relationships that dominate the behavior of the phenomena being simulated. Models require extensive empirical understandings for their formulation, and require extensive empirical data for their verification. It can be said that models without data are not compelling, and data without models are not informative.

A powerful research paradigm is based on confronting models with rigorous empirical data to test the applicability and generality of relationships, and account for the influences of spatial patterns, temporal fluctuations and time lags (Kareiva and Anderson, 1988). It is an iterative process, with models proposing relationships, data refuting or supporting models, models being refined as a result and producing new predictions to be empirically tested. Field studies should be

designed specifically to provide information needed to parameterize and test simulation models. In this effort, manipulative experiments may provide the best information, given their ability to isolate particular factors. However, the most promising area for integrating models with field data is in the area of landscape genetics (Manel et al., 2003). Simulation models can produce explicit predictions of the level of connectivity among populations across landscapes. Molecular genetics can quantify actual rates and patterns of gene flow. The intersection of these two provides a means to optimize the fit of simulation models to actual patterns of gene flow in complex landscapes. This optimization of the fit of spatial models to patterns of gene flow in real populations provides an unprecedented means to explore and understand the interactions between environmental patterns across a range of spatial scales and the connectivity of populations, which is among the most important questions in conservation biology.

6. Conservation strategies

6.1. From general to specific

A number of researchers have proposed generalized conclusions and conservation recommendations based on the observation that forest habitat area, habitat connectivity and road density are related to population persistence and population connectivity. These generalizations include that the effects of adjacent land use on amphibians can extend over large distances (Houlahan and Findlay, 2003), and that the proximity and area of upland/breeding habitat play a key role in determining occupancy (Laan and Verboom, 1990; Pope et al., 2000). It is clearly important to account for impact of uplands surrounding wetlands (Dodd and Cade, 1998; Semlitsch, 1998) as amphibian conservation often requires maintaining relatively large forest areas and relatively low road densities in the regional landscape (Houlahan et al., 2000). However, it is not clear how to translate these general understandings to specific management recommendations for individual species in any given landscape. There are large differences among amphibian species in terms of their habitat requirements and sensitivity to landscape change. Effective conservation requires specific predictions that can be applied to unique situations to produce conservation recommendations tailored to the system, species and situation.

6.2. Core area conservation

Several researchers have proposed conservation strategies based on protecting core areas based on limited adult migration and adult philopatry. For example, Bulger et al. (2003) suggested that specific protections for migrating California red-legged frogs (*Rana aurora draytoni*) were usually unwarranted and that protecting breeding sites is critical. Other researchers propose core zone widths based on adult migrations. For example, Semlitsch (1998) and Semlitsch and Bodie (2003) suggest core zones up to 218 meters for pond breeding amphibians and up to 290 meters for amphibians in general. Other researchers stress the importance of forest in core zones for persistence of spotted salamander, marbled

salamander, Jefferson's salamander (*Ambystoma jeffersonianum*), and wood frog, based on the fact that they are unlikely to persist and travel long distances in non-forest habitat (Whitford and Vinegar, 1966; Thompson et al., 1980; Douglas and Monroe, 1981; Kleeberger and Werner, 1983; deMaynadier and Hunter, 1998; Rothermel and Semlitsch, 2002). While these core zones have been advocated by some as a guide for setting biologically meaningful buffers for wetlands and riparian zones (Semlitsch and Bodie, 2003), they are insufficient as a basis for a conservation strategy for pond breeding amphibians. Any effective conservation strategy must consider more than critical core habitat for adults (Porej et al., 2004). Juvenile dispersal and habitat connectivity are at least as important (Carr and Fahrig, 2001).

6.3. Landscape-level, population-based conservation strategies

Just as it is necessary to move from site-specific to landscape-level analyses to understand the ecological relationships between amphibian populations and their environments, it is also necessary to base conservation planning on landscape-level and population-based approaches. Non-spatial conservation plans implemented at specific sites are unlikely to provide adequate conservation of populations that depend on dispersal across complex landscapes for persistence. Just as there is often a gross mismatch between the scale of ecological research and population-level responses, there is usually the same mismatch between the scale of conservation planning and the scale of population responses.

Effective conservation planning will require vast improvements in our understanding of the factors that influence vital rates, mortality and dispersal in complex landscapes. Given the urgency of the crisis facing amphibian populations (Baillie et al., 2004), it is imperative that conservation planners make the most effective use of the information currently available. This will entail extending information from empirical research on the relationships between population size, reproduction, dispersal, mortality and habitat factors across a range of scales to spatially explicit conservation proposals. These extensions can be made in a variety of ways, including through landscape genetic analysis and spatially explicit simulation models.

7. Summary

- Habitat loss and fragmentation are among the largest threats to amphibian populations.
- The extent, pattern and quality of terrestrial habitat in landscape mosaics are as important for many species as the quality of breeding sites.
- Many species of amphibians appear vulnerable to both the loss and fragmentation of nonbreeding upland habitat.
- Population connectivity appears to be a key to regional viability, and is primarily effected through juvenile dispersal.
- In fragmented landscapes, dispersal survival is often lower than required for population viability.
- The preponderance of evidence suggests that the short term impacts of habitat loss and fragmentation increase with dispersal ability.
- Species with limited dispersal abilities are equally imperiled by habitat loss and fragmentation over longer time periods.
- Combining molecular genetics and spatial modeling of organism movement provides a means to improve understanding of how habitat amounts and configurations influence dispersal, survival and population dynamics.
- Effective conservation of amphibian populations is limited by the lack of species-specific ecological knowledge, and lack of landscape-level studies of the effects of habitat loss and fragmentation on movement, survival rates, and population dynamics.
- Conservation strategies could benefit from taking multi-scale, landscape-level approaches that integrate knowledge of species biology with broad-scale evaluations of the area and accessibility of both breeding and nonbreeding habitat.

Acknowledgements

Support for this work was provided by US Department of Education Graduate Assistantships in Areas of National Need fellowship, the Organismic and Evolutionary Biology Program and Department of Natural Resources Conservation at the University of Massachusetts, and the USDA Forest Service Rocky Mountain Research Station, RWU 4201.

REFERENCES

- Alford, R.A., Richards, S.J., 1999. Global amphibian declines: a problem in applied ecology. *Annual Review of Ecology and Systematics* 30, 133–165.
- Baillie, J.E.M., Hilton-Taylor, C., Stuart, S.N., 2004. IUCN Red List of Threatened Species. A Global Species Assessment. IUCN Gland, Switzerland and Cambridge, UK.
- Balmford, A., Green, R.E., Jenkins, M., 2003. Measuring the changing state of nature. *Trends in Ecology and Evolution* 18 (7), 326–330.
- Beebee, T.J.C., Griffiths, R.A., 2005. The amphibian decline crisis: a watershed for conservation biology?. *Biological Conservation* 125, 271–285.
- Berven, K.A., Grudzien, T.A., 1990. Dispersal in the wood frog (*Rana sylvatica*): implications for genetic population structure. *Evolution* 44, 2047–2056.
- Blaustein, A.R., Chivers, D.P., Kats, L.B., Kiesecker, J.M., 2000. Effects of ultraviolet radiation on locomotion and orientation in roughskin newts (*Taricha granulosa*). *Ethology* 106, 227–234.
- Bowne, D.R., Bowers, M.A., 2004. Interpatch movements in spatially structured populations: a literature review. *Landscape Ecology* 19 (1), 1–20.
- Breden, F., 1987. The effect of post-metamorphic dispersal on the population genetic structure of Fowler's toad, *Bufo woodhousei fowleri*. *Copeia* 1987, 386–395.
- Bridges, C.M., Semlitsch, R.D., 2000. Variation in pesticide tolerance of tadpoles among and within species of Ranidae and patterns of amphibian decline. *Conservation Biology* 14, 1490–1499.
- Broomhall, S.D., Osborne, W.S., Cunningham, R.B., 2000. Comparative effects of ambient ultraviolet-B radiation on two sympatric species of Australian frogs. *Conservation Biology* 14, 420–427.

- Brown, J.H., Kodric-Brown, A., 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58, 445–449.
- Bulger, J.B., Scott, N.J., Seymour, R.B., 2003. Terrestrial activity and conservation of adult California red-legged frogs *Rana aurora draytonii* in coastal forests and grasslands. *Biological Conservation* 110 (1), 85–95.
- Carr, L.W., Fahrig, L., 2001. Effect of road traffic on two amphibian species of different vagility. *Conservation Biology* 15 (4), 1071–1078.
- Carr, L.W., Pope, S.E., Fahrig, L., 2002. Impacts of landscape transformation by roads. In: Gutzwiller, K.J. (Ed.), *Concepts and Applications of Landscape Ecology in Biological Conservation*. Springer-Verlag, New York.
- Curtis, J.M.R., Taylor, E.B., 2004. The genetic structure of coastal giant salamander (*Dicamptodon tenebrosus*) in a managed forest. *Biological Conservation* 115 (1), 45–54.
- Cushman, S.A., McGarigal, K., 2003. Hierarchical, multi-scale decomposition of species-environment relationships. *Landscape Ecology* 17, 637–646.
- Cushman, S.A., McGarigal, K., 2004. Hierarchical analysis of forest bird species-environment relationships in the Oregon Coast Range. *Ecological Applications* 14 (4), 1090–1105.
- Davidson, C., Shaffer, H.B., Jennings, M.R., 2001. Declines of the California red-legged frog: climate, UV-B, habitat, and pesticides hypotheses. *Ecological Applications* 11, 464–479.
- Delis, P.R., Mushinsky, H.R., McCoy, E.D., 1996. Decline of some west-central Florida anuran populations in response to habitat degradation. *Biodiversity and Conservation* 5, 1579–1595.
- deMaynadier, P.G., Hunter Jr., M.L., 1998. Effects of silvicultural edges on distribution and abundance of amphibians in Maine. *Conservation Biology* 12 (2), 340–352.
- deMaynadier, P.G., Hunter Jr., M.L., 1999. Forest canopy closure and juvenile emigration by pool-breeding amphibians in Maine. *Journal of Wildlife Management* 63, 441–450.
- deMaynadier, P.G., Hunter Jr., M.L., 2000. Road effects on amphibian movements in a forested landscape. *Natural Areas Journal* 20, 56–65.
- Dodd Jr., C.K., Cade, B.A., 1998. Movement patterns and the conservation of amphibians breeding in small, temporary wetlands. *Conservation Biology* 12, 331–339.
- Douglas, M.E., Monroe, B.L., 1981. A comparative study of topographical orientation in *Ambystoma* (Amphibia: Caudata). *Copeia* 1981, 460–463.
- Dupuis, L.A., Steventon, D., 1999. Riparian management and the tailed frog in northern coastal forests. *Forest Ecology and Management* 124, 35–43.
- Edenham, P., 1996. Spatial dynamics of the European tree frog (*Hyla arborea* L.) in a heterogeneous landscape. Dissertation, Swedish University of Agricultural Sciences, Uppsala.
- Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? *Ecological Modelling* 105, 273–292.
- Fahrig, L., 2001. How much habitat is enough? *Biological Conservation* 100, 65–74.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Reviews of Ecology and Systematics* 34, 487–515.
- Fahrig, L., Pedlar, J.H., Pope, S.E., Taylor, P.D., Wegner, J.F., 1995. Effect of road traffic on amphibian density. *Biological Conservation* 73, 177–182.
- Findlay, C.S., Houlihan, J., 1997. Anthropogenic correlates of species richness in southeastern Ontario wetlands. *Conservation Biology* 11, 1000–1009.
- Forester, D.C., Lykens, D.V., 1991. Age structure in a population of red-spotted newts from the Allegheny plateau of Maryland. *Journal of Herpetology* 25, 373–376.
- Funk, W.C., Blouin, M.C., Cron, P.S., Stephen, Maxell, B.A., Pilliod, D.S., Amish, S., Allendorf, F.W., 2005. Population structure of Columbia spotted frogs (*Rana luteiventris*) is strongly affected by the landscape. *Molecular Ecology* 14, 483–496.
- Gibbs, J.P., 1998. Amphibian movements in response to forest edges, roads, and streambeds in southern New England. *Journal of Wildlife Management* 62, 584–589.
- Gill, D.E., 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). *Ecological Monographs* 48, 145–166.
- Grand, J., Cushman, S.A., 2003. A multiple-scale analysis of species-habitat relationships: breeding birds in a pitch pine-scrub oak (*Pinus rigida*-*Quercus ilicifolia*) community. *Biological Conservation* 112 (3), 307–317.
- Guerry, A.D., Hunter Jr., M.L., 2002. Amphibian distributions in a landscape of forests and agriculture: an examination of landscape composition and configuration. *Conservation Biology* 16, 745–754.
- Harrison, S., 1991. Local extinction in a metapopulation context: an empirical evaluation. In: Gilpin, M.E., Hanski, I. (Eds.), *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London, pp. 73–88.
- Hazell, D., 2003. Frog ecology in modified Australian landscapes: a review. *Wildlife Research* 30 (3), 193–205.
- Hecnar, S.J., 1995. Acute and chronic toxicity of ammonium nitrate fertilizer to amphibians from southern Ontario. *Environmental Toxicology and Chemistry* 14, 2131–2137.
- Hecnar, S.J., M'Closkey, R.T., 1996. Regional dynamics and the status of amphibians. *Ecology* 77, 2091–2097.
- Hecnar, S.J., M'Closkey, R.T., 1997. The effects of predatory fish on amphibian species richness and distribution. *Biological Conservation* 79, 123–131.
- Houlihan, J.E., Findlay, C.S., 2003. The effects of adjacent land use on wetland amphibian species richness and community composition. *Canadian Journal of Fisheries and Aquatic Sciences* 60, 1078–1094.
- Houlihan, J.E., Findlay, C.S., Schmidt, B.R., Meyer, A.H., Kuzmin, S.L., 2000. Quantitative evidence for global amphibian population declines. *Nature* 404, 752–755.
- Kareiva, P., Anderson, M., 1988. Spatial aspects of species interactions: the wedding of models and experiments. In: Hastings, A. (Ed.), *Community Ecology*. Springer-Verlag, New York, pp. 35–50.
- Kiesecker, J.M., Blaustein, A.R., Belden, L.K., 2001. Complex causes of amphibian population declines. *Nature* 410, 681–684.
- Kleeberger, S.R., Werner, J.K., 1983. Post-breeding migration and summer movement of *Ambystoma maculatum*. *Journal of Herpetology* 17, 176–177.
- Knutson, M.G., Sauer, J.R., Olsen, D.A., Mossman, M.J., Hemesath, L.M., Lannoo, M.J., 1999. Effects of landscape composition and wetland fragmentation on frog and toad abundance and species richness in Iowa and Wisconsin, USA. *Conservation Biology* 13, 1437–1446.
- Kolozsvary, M.B., Swihart, R.K., 1999. Habitat fragmentation and the distribution of amphibians, patch and landscape correlates in farmland. *Canadian Journal of Zoology* 77, 1288–1299.
- Laan, R., Verboom, B., 1990. Effects of pool size and isolation on amphibian communities. *Biological Conservation* 54, 251–262.
- Lande, R., 1988. Genetics and demography in biological conservation. *Science* 241, 1455–1460.
- Lawton, J.H., May, R.M., 1995. *Extinction Rates*. Oxford University Press.
- Lehtinen, R.M., Galatowitsch, S.M., Tester, J.R., 1999. Consequences of habitat loss and fragmentation for wetland amphibian assemblages. *Wetlands* 19 (1), 1–12.
- Litvaitis, J.A., Titus, K., Anderson, E.M., 1994. Measuring vertebrate use of terrestrial habitats and foods. In: Bookhout, T.A. (Ed.), *Research and Management Techniques for Wildlife and Habitats*, fifth ed. The Wildlife Society, Bethesda, Maryland, USA, pp. 254–270.

- Madison, D.M., 1997. The emigration of radio-implemented Spotted Salamanders, *Ambystoma maculatum*. *Journal of Herpetology* 31, 542–551.
- Manel, S., Schwartz, M.K., Luikart, G., Taberlet, P., 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends in Ecology and Evolution* 18 (4), 189–197.
- Marsh, D.M., Thakur, K.A., Bulka, K.C., Clarke, L.B., 2004. Dispersal and colonization through open fields by a terrestrial, woodland salamander. *Ecology* 85 (12), 3396–3405.
- Marsh, D.M., Trenham, P.C., 2001. Metapopulation dynamics and amphibian conservation. *Conservation Biology* 15, 40–49.
- McGarigal, K., Cushman, S.A., 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* 12 (2), 335–345.
- Monkkonen, M., Reunanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84, 302–305.
- Myers, N., Knoll, A.H., 2001. The biotic crisis and the future of evolution. *Proceedings of the National Academy of Science* 98 (10), 5389–5392.
- Newcomb Homan, R., Windmiller, B.S., Reed, J.M., 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* 14 (5), 1547–1553.
- Pechmann, J.H.K., Scott, R.D., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., Gibbons, J.W., 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253, 892–895.
- Petranka, J.W., Smith, C.K., Scott, A.F., 2004. Identifying the minimal demographic unit for monitoring pond-breeding amphibians. *Ecological Applications* 14 (4), 1065–1078.
- Pope, S.E., Fahrig, L., Merriam, H.G., 2000. Landscape complementation and metapopulation effects on leopard frog populations. *Ecology* 81, 2498–2508.
- Porej, D., Micacchion, M., Hetherington, T.E., 2004. Core terrestrial habitat for conservation of local populations of salamanders and wood frogs in agricultural landscapes. *Biological Conservation* 120, 399–409.
- Pounds, J.A., Fogden, M.P.L., Campbell, J.H., 1999. Biological response to climate change on a tropical mountain. *Nature* 398, 611–615.
- Preisser, E.L., Kefer, J.Y., Lawrence, J.D., 2001. Vernal pool conservation in Connecticut: an assessment and recommendations. *Environmental Management* 26 (5), 503–513.
- Regosin, J.V., Windmiller, B.S., Reed, M.J., 2003. Terrestrial habitat use and winter densities of the wood frog (*Rana sylvatica*). *Journal of Herpetology* 37, 390–394.
- Reh, W., Seitz, A., 1990. The influence of land use on the genetic structure of populations of the common frog (*Rana temporaria*). *Biological Conservation* 54, 239–249.
- Rothermel, B.B., 2004. Migratory success of juveniles: a potential constraint on connectivity for pond-breeding amphibians. *Ecological Applications* 14 (5), 1535–1546.
- Rothermel, B.B., Semlitsch, R.D., 2002. An experimental investigation of landscape resistance of forest versus old-field habitats to emigrating juvenile amphibians. *Conservation Biology* 16, 1324–1332.
- Ruggiero, L.F., Hayward, G.D., Squires, J.R., 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. *Conservation Biology* 8 (2), 364–372.
- Schwartz, M.K., Tallmon, D.A., Luikart, G., 1998. Review of DNA-based census and effective population size estimators. *Animal Conservation* 1 (4), 293–299.
- Semlitsch, R.D., 1998. Critical elements for biologically based recovery plans of aquatic-breeding amphibians. *Conservation Biology* 16, 619–629.
- Semlitsch, R.D., 2000. Principles for management of aquatic-breeding amphibians. *Journal of Wildlife Management* 64, 615–631.
- Semlitsch, R.D., Bodie, J.R., 1998. Are small, isolated wetlands expendable? *Conservation Biology* 12 (5), 1129–1133.
- Semlitsch, R.D., Bodie, J.R., 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. *Conservation Biology* 17, 1219–1228.
- Semlitsch, R.D., Scott, D.E., Pechmann, J.H.K., Gibbons, J.W., 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. In: Cody, P.M.L., Smallwood, J.A. (Eds.), *Long-Term Studies of Vertebrate Communities*. Academic Press, San Diego, CA, USA, pp. 217–248.
- Sinsch, U., 1990. Migration and orientation in anuran amphibians. *Ethology, Ecology and Evolution* 2, 65–79.
- Sinsch, U., 1992. Structure and dynamics of a natterjack toad metapopulation (*Bufo calamita*). *Oecologia* 90, 489–499.
- Sinsch, U., 1997. Postmetamorphic dispersal and recruitment of first breeders in a *Bufo calamita* metapopulation. *Oecologia* 112, 42–47.
- Sinsch, U., Seidel, D., 1995. Dynamics of local and temporal breeding assemblages in a *Bufo calamita* metapopulation. *Australian Journal of Ecology* 20, 351–361.
- Sjögren, P., 1991. Extinction and isolation gradients in metapopulations: the case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society* 42, 135–148.
- Sjögren-Gulve, P., 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. *Ecology* 75, 1357–1367.
- Sjögren-Gulve, P., 1998. Spatial movement patterns in frogs: target-oriented dispersal in the pool frog, *Rana lessonae*. *Ecoscience* 5, 31–38.
- Skelly, D.K., Werner, E.E., Cortwright, S.A., 1999. Long-term distributional dynamics of a Michigan amphibian assemblage. *Ecology* 80, 2326–2337.
- Stebbins, R.C., Cohen, N.W., 1995. *A Natural History of Amphibians*. Princeton University Press, Princeton, NJ, USA. 316 pp.
- Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., Waller, R.W., 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306, 1783–1786.
- Taylor, B.E., Scott, D.E., 1997. Effects of larval density dependence on population dynamics of *Ambystoma opacum*. *Herpetologica* 53, 132–145.
- Thompson, E.L., Gates, J.E., Taylor, G.J., 1980. Distribution and breeding habitat selection of Jefferson Salamander *Ambystoma jeffersonianum* in Maryland. *Journal of Herpetology* 14, 113–120.
- Trenham, P.C., Koenig, W.D., Mossman, M.J., Stark, S.L., Jaegger, L.A., 2003. Regional dynamics of wetland-breeding frogs and toads: turnover and synchrony. *Ecological Applications* 13 (6), 1522–1532.
- Trenham, P.C., Shaffer, H.B., 2005. Amphibian upland habitat use and its consequences for population viability. *Ecological Applications* 15 (4), 1158–1168.
- Trenham, P.C., Shaffer, H.B., Koenig, W.D., Stromberg, M.R., 2000. Life history and demographic variation in the California tiger salamander (*Ambystoma californiense*). *Copeia* 2000, 365–377.
- Vallan, D., 2000. Influence of forest fragmentation on amphibian diversity in the nature reserve of Amohitantly, highland Madagascar. *Biological Conservation* 96, 31–43.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. *Science* 277, 494–499.
- Vos, C.C., Chardon, J.P., 1998. Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. *Journal of Applied Ecology* 35, 44–56.

- Weyrauch, S.L., Grubb Jr., T.C., 2004. Patch and landscape characteristics associated with the distribution of woodland amphibians in an agricultural fragmented landscape: an information-theoretic approach. *Biological Conservation* 115, 443–450.
- Whitford, W.G., Vinegar, A., 1966. Homing, survivorship, and overwintering of larvae in Spotted salamanders, *Ambystoma maculatum*. *Copeia* 1966, 515–519.
- Wiens, J.A., 1989. Spatial scaling in ecology. *Functional Ecology* 3, 385–397.
- Wilson, E.O., 1999. *The Diversity of Life*. Longitude, New York, USA.
- Windmiller, B.S., 1996. The pond, the forest, and the city: spotted salamander ecology and conservation in human-dominated landscape. Ph.D. Dissertation, Tufts University, Boston, Massachusetts.